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THE DECISIVE INFLUENCE OF LATE WINTER WEATHER ON WHEAT LEAF RUST EPIPHYTOTICS

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THE DECISIVE INFLUENCE OF LATE WINTER WEATHER ON WHEAT LEAF RUST EPIPHYTOTICS

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On the basis of an analysis of winter and spring weather during 23 years of severe, moderate, and light wheat leaf rust (Puccinia triticina Eriks.) infection in Oklahoma (Pl. Dis. Rep. 26:213-217), the writer in 1942 suggested that leaf rust epiphytotics might be predicted by the end of March in Oklahoma, a time at which leaf rust is ordinarily inconspicuous, 2 1/2 months before harvest, in ample time to permit a modification of spring planting plans when a severe rust epiphytotic threatens. The basis for such prediction is an analysis of winter and March temperatures and precipitation, and disregards the weather of April, May, and June, the months during which leaf rust attack becomes apparent to the casual observer.

The purpose of this report is to present findings with reference to several cognate problems, viz. (1) application of the method of leaf rust prediction in the 1942 and 1943 seasons in Oklahoma, (2) suitability of the method for more northern parts of the United States, and (3) explanation of the significance of the December-March period and the non-significance of the April-June period in Oklahoma (or the counterparts of these periods in other latitudes) in terms of the annual cycle of leaf rust.

In the May 15, 1942 issue of the Plant Disease Reporter, on the basis of exceptionally dry weather from December through March, and despite a record-breaking April rainfall for Oklahoma of 8.31 inches, the writer predicted that 1942 would not be a year of severe leaf rust. That this opinion was not shared by other workers, who were impressed by the heavy April rainfall at the time the rust was appearing, is evidenced by a report from Kansas dated May 22 (Pl. Dis. Rep. 26:240) that "there is evidence that another severe epiphytotic of leaf rust of wheat is rapidly developing in the southern and central plains area." On June 15, however, the writer's prediction of a month before was borne out, when the Kansas report of that date stated that "the threatened leaf rust epiphytotic on winter wheat in Kansas failed to materialize, owing to unusually cold weather during May and early June." The fact that 1942 proved to be a light rust year in Kansas, Oklahoma, and Texas was well established by harvest time, but that this was due to cold weather in May and early June is not borne out by the facts. The official weather report for Kansas in 1942 indicates that the average temperature for May was 63.2°F. (comparing with the long-time average of 64.0°F.) and for June 72.7°F. (comparing with the long-time average of 73.8°F.). The temperatures were thus within about one degree of the normal temperatures for these months, and they could have been much lower without falling below the optimum range for wheat leaf rust multiplication (55-75°F.).

According to the late winter weather, 1943 was destined to be another year of slight leaf rust damage in Oklahoma (See Table 1). Despite a mild winter, the average temperature for March was 46.0°F., which is 4.6° below normal and well below the optimum for leaf rust multiplication. Moreover the total precipitation for January through March was only 2.72 inches, which is 54 percent of normal. There was nearly as much rain in April as in the three previous months combined, while May had a record-breaking 10.27 inches of rain. The 1943 season did prove to be a year of minor leaf rust damage. By harvest time wheat was conspicuously infected but the attack was too late to result in more than a trace of crop loss.

In both years, the fears of crop observers that failed to materialize were based on observation of weather conditions in April and May. All available evidence indicates that in the Southwest the conditions that determine the severity of leaf rust are those of December through March, and the 1942 and 1943 seasons both bear out the writer's hypothesis that in this latitude the weather from April onward will rarely, if ever, prevent an epiphytotic provided the late winter has been favorable, or permit an epiphytotic if the late winter has been unfavorable for rust. Reasons for this will be indicated presently.

It is of particular interest to determine whether the decisive influence of late winter weather on wheat leaf rust in the southern Great Plains has its counterpart in more northern parts of the wheat belt. A priori one would not necessarily anticipate that this would be the case, since the annual cycle of leaf rust in the North occurs under conditions that very somewhat from those in the Southwest. In the North there is less abundant over-intering of the rust, owing to lower winter temperatures. Spring renewal of the rust is later, and is influenced to a greater extent than in the South by uredospores that are blown northward from the earlier infected fields of the South.

To investigate this point, the States of Illinois and Iowa were selected for comparison with Oklahoma, since they are sufficiently far to the north that their seasons are almost exactly one month later than that of Oklahoma, which simplifies comparison on the basis of average monthly temperatures, the month of March in Oklahoma corresponding phenologically to the month of April in Illinois and Iowa[1]. The principal years of severe leaf rust damage, and the principal years of very light leaf rust, according to reports in the Plant Disease Reporter, were selected for each State, excluding years of conflicting reports or of serious complication with stem rust. The pertinent weather data for late winter and spring in each of these years are tabulated in Table 1, the corresponding seasons being considered one month later in Iowa and Illinois than in Oklahoma. For Illinois the years 1922-1926 were included because particularly detailed data are available regarding the severity of leaf rust in Illinois during those years[2].

1/ Note in Table 1 that the long-time average temperature for March in Oklahoma differs by less than 2°F. from the long-time average temperature for April in Illinois and Iowa.

2/ Tehon, L. R. Epidemic diseases of grain crops in Illinois, 1922-1926. The measure of their prevalence and destructiveness and an interpretation of weather relations based on wheat leaf rust data. Ill. Nat. Hist. Surv. 17:1-96. 1927

Considering first the years of severe rust, the average temperatures of late winter in all years for all States were normal or above normal, often considerably above. The average temperature for March in Oklahoma and April in Illinois and Iowa in all cases was normal or warmer than normal. For the period up to April 1 in Oklahoma and May 1 in Illinois and Iowa, in each of these years of severe rust the precipitation was normal or above normal. If now we turn to the spring months in which leaf rust becomes obvious, April and May in Oklahoma, and May and June in the more northern States, we find a striking lack of any correlation between temperature or precipitation and rust severity. In three of the years of severe rust in Oklahoma and in one year each in Illinois and Iowa, the spring period was abnormally dry, while in 4 other years of leaf rust epiphytotics the spring was abnormally wet. With one exception, 1935 in Illinois, the temperatures of these spring months were normal.

In regard to the years of light rust, abnormally low winter temperatures in 1936 in Illinois and Iowa were associated with poor rust development. In four additional cases the average temperature of March in Oklahoma or April in the North was clearly a limiting factor in rust development, these low average temperatures (43.2°F. to 46.9°F.) being well below the optimal range for leaf rust uredospore germination. Even more striking is the correlation between deficient precipitation in the late winter period and subsequent lack of rust intensity. In 14 out of the 17 years of light rust, the late winter period was characterized by a deficit in normal precipitation ranging from 73 percent to 20 percent. The three years of light rust with only minor moisture deficits in late winter were 3 of the 4 years with abnormally low temperatures in March (Oklahoma) or April (Illinois, Iowa). Hence, every year of light rust was a year characterized by deficient late winter moisture or abnormally low late winter temperatures or both, and no year of severe rust was so characterized. In the years of light rust, as in those of severe rust, there is again no correlation with either abnormal temperatures or abnormal precipitation during the spring months. Little rust occurred whether the April-May period in Oklahoma or the corresponding May-June period in Illinois and Iowa experienced 12.60 inches of rain (Oklahoma, 1943, a 55 percent excess) or 3.73 inches (Illinois, 1936, less than one-half normal) or any excess or deficit between these extremes. There were few departures from normal temperatures during the spring months of these years of light rust and even these were without significance since, both in the 14 normal years and the 3 years with temperature departures greater than 3.5°F., the average temperatures for the two spring months were within the range of optimal leaf rust development (55°-75°F.).

Consider now the mean temperature and moisture conditions for the years of severe rust in comparison with those of light rust for each State individually. It is seen that on the average the years of severe rust have average late winter temperatures up to 4.9° higher, and March (Oklahoma) or April (Illinois, ~~to a~~) temperatures slightly higher than the years of light rust, and in particular the severe rust years have late winter precipitations that are almost or more than double those of the years of light rust. On the contrary, there is comparatively little difference in

		Years of Severe Rust					Years of Light Rust					
State	Year	Temp. Dec.-Feb.	Temp. Mar.	Temp. Apr.-May	Pptn. Jan.-Mar.	Pptn. Apr.-May	Year	Temp. Dec.-Feb.	Temp. Mar.	Temp. Apr.-May	Pptn. Jan.-Mar.	Pptn. Apr.-May
Oklahoma	1919	40.27	51.2	62.75	4.55	8.68	1924	40.17	43.2	61.90	4.96	6.65
	1921	43.53	57.0	64.55	6.64	5.80	1925	39.53	56.1	67.05	2.63	6.88
	1922	41.37	50.1	64.95	10.07	12.22	1936	36.13	56.3	66.10	1.33	5.48
	1927	42.37	50.7	67.65	6.30	9.01	1937	39.40	46.9	65.90	4.86	5.73
	1934	43.90	49.5	66.25	4.74	5.26	1940	37.33	53.0	64.05	3.44	8.90
	1935	42.90	57.40	61.75	6.24	9.76	1942	40.60	50.7	64.90	3.34	10.52
	1938	42.43	58.10	64.10	10.15	8.83	1943	42.2	46.0	65.6	2.72	12.60
	1939	41.77	54.1	65.65	6.28	6.20						
Mean		42.32	53.5	64.71	6.87	8.22		39.34	50.3	65.07	3.33	8.11
50-yr.av.		38.51	50.6	64.20	5.01	8.14		38.51	50.6	64.20	5.01	8.14
Mean:50-yr. average		+3.81°	+2.9°	+.51°	-33%	+1%		+.83°	-.4°	+.87°	-33%	-.3%

State	Year	Temp. Dec.-Mar.	Temp. Apr.	Temp. May-June	Pptn. Feb.-Apr.	Pptn. May-June	Year	Temp. Dec.-Mar.	Temp. Apr.	Temp. May-June	Pptn. Feb.-Apr.	Pptn. May-June
Illinois	1922	38.9	52.1	70.20	12.77	5.08	1924	28.6	54.0	63.45	6.36	10.35
	1923	34.4	60.9	67.05	8.77	7.88	1925	33.9	58.6	67.00	6.84	6.37
	1935	36.6	49.7	62.95	6.74	13.77	1926	32.0	46.4	66.55	8.12	6.39
	1938	36.3	54.4	66.80	11.13	10.37	1930	33.0	55.6	67.95	6.26	5.21
	1939	35.1	49.6	69.90	11.68	7.57	1934	33.2	53.3	73.45	5.02	4.09
							1936	27.6	49.0	70.10	6.02	3.73
Mean		36.3	53.3	67.38	10.62	8.93		31.4	52.8	68.08	6.44	6.02
50-yr. av.		31.6	52.2	67.10	8.61	8.15		31.6	52.2	67.10	8.61	8.15
Mean:50- yr. average		+4.7°	+1.1°	+.28°	+23%	+9.6%		-.2°	+.6°	+.98°	-25%	-26%
Iowa	1927	28.5	49.2	62.40	7.92	7.11	1931	31.5	50.9	66.25	4.23	6.69
	1929	23.0	51.2	62.65	7.38	5.55	1932	28.5	50.0	67.15	4.26	9.16
	1938	29.1	50.3	64.35	6.96	10.11	1933	28.2	48.8	69.15	4.63	6.00
							1936	19.3	45.9	68.15	3.46	5.76
Mean		26.9	50.2	63.13	7.42	7.59		26.9	48.9	67.68	4.15	6.90
50-yr. av.		24.9	48.7	64.90	6.54	8.69		24.9	48.7	64.90	6.54	8.69
Mean:50-yr. average		+2°	+1.5°	-1.77°	+13%	-13%		+2°	+.2°	+2.78°	-37%	-20%

the mean spring temperatures or precipitations between the years of severe rust and those of light rust for each state.

It was hoped to discover, in absolute terms of temperature and precipitation, the conditions favoring or inhibiting leaf rust development regardless of latitude. This has not been possible. For example epiphytotics occurred in Oklahoma when the January-March precipitation was 4.55 (1919) and 4.75 (1934) inches, values that for Oklahoma are not significantly subnormal, while in Illinois, where the normal precipitation for the same phenological period is much higher, years of light rust were associated with late winter precipitations of 5 to 7 inches, amounts that are significantly deficient for Illinois but would represent excessive late winter precipitation in Oklahoma. Iowa is intermediate in this respect.

The greater amounts of precipitation necessary to induce a leaf rust epiphytotic in Illinois are not due to higher average temperatures, which would readily dissipate the moisture. For corresponding phenologic periods the temperatures in Illinois and Oklahoma are very similar.

The more probable explanation of this apparent difference in effect on rust of the absolute levels of precipitation deficits among the three States is a psychological one. In Illinois, where the average winter and spring precipitation considerably exceeds that of Oklahoma, wheat leaf rust on the average can be expected to be more severe. Estimates of crop damage by diseases, as reported in the Plant Disease Reporter, are for the most part the estimates of men whose observations are confined to a single State. If a disease occurs in a given State, e.g. Illinois, with great regularity and causes a greater or less amount of damage almost every year, the disease would doubtless be considered "light" when it was actually much more destructive than the same severity of the disease would be considered in a State, e.g. Oklahoma, in which, due to different climatic conditions, the disease is normally less destructive. In other words, referring to Table 1, the amount of and damage from leaf rust in Oklahoma in 1927, a "severe" rust year for Oklahoma, associated with an excessive late winter rainfall for Oklahoma (6.30"), might be almost identical with the amount of and damage from leaf rust in Illinois in 1930, a "light" rust year for Illinois, associated with a deficient late winter rainfall for Illinois (6.26"). But since Oklahoma would record this as a "severe" rust year and Illinois would call it a "light" rust year, each term being correct for the confines and normal conditions of the State involved in each case, it becomes necessary to consider each State individually in interpreting leaf rust epiphytology. The principle that deficient warmth and precipitation in late winter inhibit rust applies equally in each of the States considered here, but the amount of precipitation that is considered deficient in one State may be excessive in another. An analogous case is the classification of American Upland

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Table 1. Average temperatures and total precipitation in Oklahoma, Illinois, and Iowa during the late winter and early spring in the principal years of severe and of light wheat leaf rust in each State. (Figures from U.S. Weather Bureau.) Precipitations underscored are 20% greater (dotted underscoring) or less (solid underscoring) than 50-year average. Temperatures underscored are 3 1/2°F. greater (dotted underscoring) or less (solid underscoring) than 50-year average.

cotton varieties as "susceptible" to angular leaf spot in the parts of the world where highly resistant Asiatic cottons are grown, while the Upland varieties are classed as "resistant" in areas where the very susceptible Sea Island varieties are cultivated.

It seems almost paradoxical that the weather at the time when leaf rust is readily apparent in wheat fields has little to do with its ensuant damage, while the weather at a period during which rust can be found only by long and patient search is dominant in influencing its subsequent destruction. Almost without exception, crop observers have attempted to correlate rust damage with the weather occurring after the rust has made its obvious appearance, and, as illustrated above in the discussion of the years 1942 and 1943 in the Southwest, in many cases these attempts have led to entirely erroneous conclusions. A striking example of this is seen in Tehon's study of wheat leaf rust in Illinois during the 5-year period 1922-1926[1]. The three years of "destructive rust" were, respectively, years in which the May-June period (that period in which rust becomes apparent, and which, according to the foregoing analysis is immaterial in relation to rust development) was in one case dry and hot, in a second case wet and cold, and in the third case normal for temperature and precipitation. The two years in which rust was not destructive were years in which the rainfall was only very slightly below normal and the temperatures were normal during the May-June period. Tehon concludes that serious rust is associated with either dry-hot or wet-cold weather. Reference to Table 1, which includes those years for Illinois shows that this paradoxical situation is readily clarified by reference to the late winter weather, in which the years of light rust were years of deficient moisture or low temperatures in February-April.

The explanation of the decisive influence of late winter weather and the negligible influence of spring weather on leaf rust destructiveness can be found by examining the details of the annual cycle of the fungus and its environmental requirements.

Puccinia triticina (P. rubigo-vera var. tritici) overwinters as mycelium in winter wheat with occasional uredial multiplication during warm periods in the winter. Alternate hosts play no part in the overwintering of the leaf rust fungus in the United States. On the average, in late winter, one may expect to find leaf rust persisting to the extent of one uredinium per 10 to one per 1000 leaves, the amount being negatively correlated with the severity of the winter, resulting in winterkilling of the wheat leaves and hence of the fungus, and positively correlated with mild periods in the winter, which permit occasional rust multiplication, and winter precipitation which is essential to such multiplication, or which falls as a snow cover that protects infected leaves from destruction by freezing. The combination of these influences will determine the extent of overwintering whether to the extent of one pustule per 10 leaves or one per 10,000.

Rust ordinarily is not noticeable to the casual observer until it has reached the intensity of at least 1 pustule per leaf. This will be on the "first date of observation" which on the average is in early April in Oklahoma, and May or early June in the latitude of Illinois and

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[1] l.c., fig. 101, p. 89, legend and pertinent discussion.

Indiana and slightly later in Iowa, i.e. at the end of the period of late winter weather that is essential to rust destructiveness. We may divide the course of spring renewal of leaf rust into two distinct phases: (1) the late winter phase, in which the rust increases from the least amount that overwinters (e.g. 1 pustule per 100, 1000, or 10,000 leaves) to the amount of rust that first becomes readily noticeable (approximately 1 pustule per leaf); and (2) the spring phase in which the rust increases from the first noticeable amount to its maximum for the season, which may be somewhat more than 1000 pustules per leaf. Each of these phases involves several successive generations of uredial multiplication, and it is important to note that rust multiplication proceeds as a logarithmic progression (x pustules $\rightarrow x^2$ pustules $\rightarrow x^3$ pustules $\rightarrow x^4$ pustules, etc.) in which the first generations of multiplication in late winter (e.g. from 1 pustule per 1000 leaves to 1 pustule per leaf) have fully the importance of the spring generations (e.g. from 1 pustule per leaf to 1000 pustules per leaf).

The late winter generations must occur in the presence of weather that is close to the lower thresholds for rust survival and reproduction. This is particularly noticeable in the last month of the late winter period, March in Oklahoma and April in Illinois and Iowa. During this month long-time average temperatures are from 48.7° to 52.2°F. in the 3 States. It is axiomatic that in growth and reproduction organisms respond most strikingly to minor variations in any environmental factor when the intensity of that factor is the least or most that can be borne without serious injury to the organism, i.e. when it is at a threshold level. A temperature of 50°F. is of such an intensity, for with a slight increase above 50°F. we reach the range of optimal leaf rust multiplication, while with a corresponding decrease below 50°F. the temperature becomes definitely unfavorable for leaf rust. Marshall Ward reported that the minimum temperature for satisfactory uredospore germination of P. triticina is 10°C. (= 50°F.). Moreover, several workers have noted with reference to the length of the incubation period of P. triticina that this period is about 7 days at optimal temperatures but that at lower temperatures it requires 10 to 12 days (Yarkina) or even 20 days in winter in India (Mehta). Thus temperatures even slightly below the averages for the last month of the late winter period are doubly inhibitory to leaf rust, and temperatures slightly above the average are doubly beneficial to it.

Similarly the precipitation of the late winter months is markedly less than that of the spring months in each of the States considered here. In addition the rust during the winter may be subjected to extremes of cold that in a single night may reduce the rust population by 9/10 or 99/100, thus necessitating additional generations of multiplication in order to reach the concentration it had before the freezing weather.

In all of these particulars we find that during the late-winter phase, the leaf rust organism lives a precarious existence in an environment in which slight departures from normal will turn the balance in the favor of or against the survival and increase of the rust. And since several generations of rust multiplication must occur in late winter if the disease is to reach epiphytotic proportions in the spring, it is

readily apparent why the late winter weather is decisive in influencing leaf rust epiphytotics.

Quite the reverse is the case in the spring months, April and May in Oklahoma and May and June in Illinois and Iowa. In the 33 years of severe and light rust indicated in Table 1, in no instance did the average temperature for the spring months lie outside the optimal range for leaf rust development. Furthermore, since these months are normally rainy months, we find that even in the seasons in which the spring rainfall drops below the long-time average, moisture still is plentiful, in comparison with the normal for the late winter months, and ample for leaf rust development in practically every year. Moreover, in the spring months, in contrast to the winter ones, leaf rust multiplication is not entirely dependent on repeated uredial generations in any given area of the Great Plains, since in the spring there are two sources of inoculum, uredospores produced locally and those that are brought in by the wind from more southern fields.

Thus the spring months, those in which rust becomes apparent, have little effect in deciding the destructiveness of leaf rust in any given year. The weather conditions in these months are regularly within the range favoring rust development, and hence we can understand the reason for the lack of correlation between spring weather and rust intensity that is evident from Table 1 and from the data of Tehon and those of the 1942 and 1943 seasons in the Southwest. The destructiveness of leaf rust appears to be a direct function of its intensity at the close of the late winter period (April 1 in Oklahoma, May 1 in Illinois and Iowa) and this intensity in turn depends on the extent to which the temperatures and precipitation of the late winter period have permitted winter survival and successive generations of multiplication up to the opening of the spring period. This situation is shown diagrammatically in Figure 1.

In the figure the critical late winter and non-critical spring periods are indicated. In the latter there is no variation in the slopes of the curves of rust intensity in accordance with the conclusion that rust multiplication proceeds fairly regularly during this period in virtually all seasons, since both moisture and temperatures are regularly within a broad optimal range. The intensity of ultimate rust development and the extent to which it causes crop loss, are direct results of the degree of infection on April 1 (for Oklahoma), which, as shown in the figure, depends first on the extent of reduction of infection due to winter killing (curves from December to March 1) and second on the extent to which March temperatures and precipitation are favorable. While the values for rust intensity and the slope of the curve of a "normal rust year" have been arbitrarily selected, they approximate the actual values and slope for Oklahoma. Thus in the "normal year" in Oklahoma one can find about 1 rust pustule per 10 leaves on March 1, which increases to about 1 pustule per leaf by April 1, and to about 1000 pustules per leaf just before maturity of the crop, producing a crop loss of 5 percent. In the epiphytotic year 1938 the rust was very conspicuous on April 2. The uppermost leaf reached the 1000-pustule stage at or shortly after heading of the wheat, and the crop loss was estimated at 29 percent.

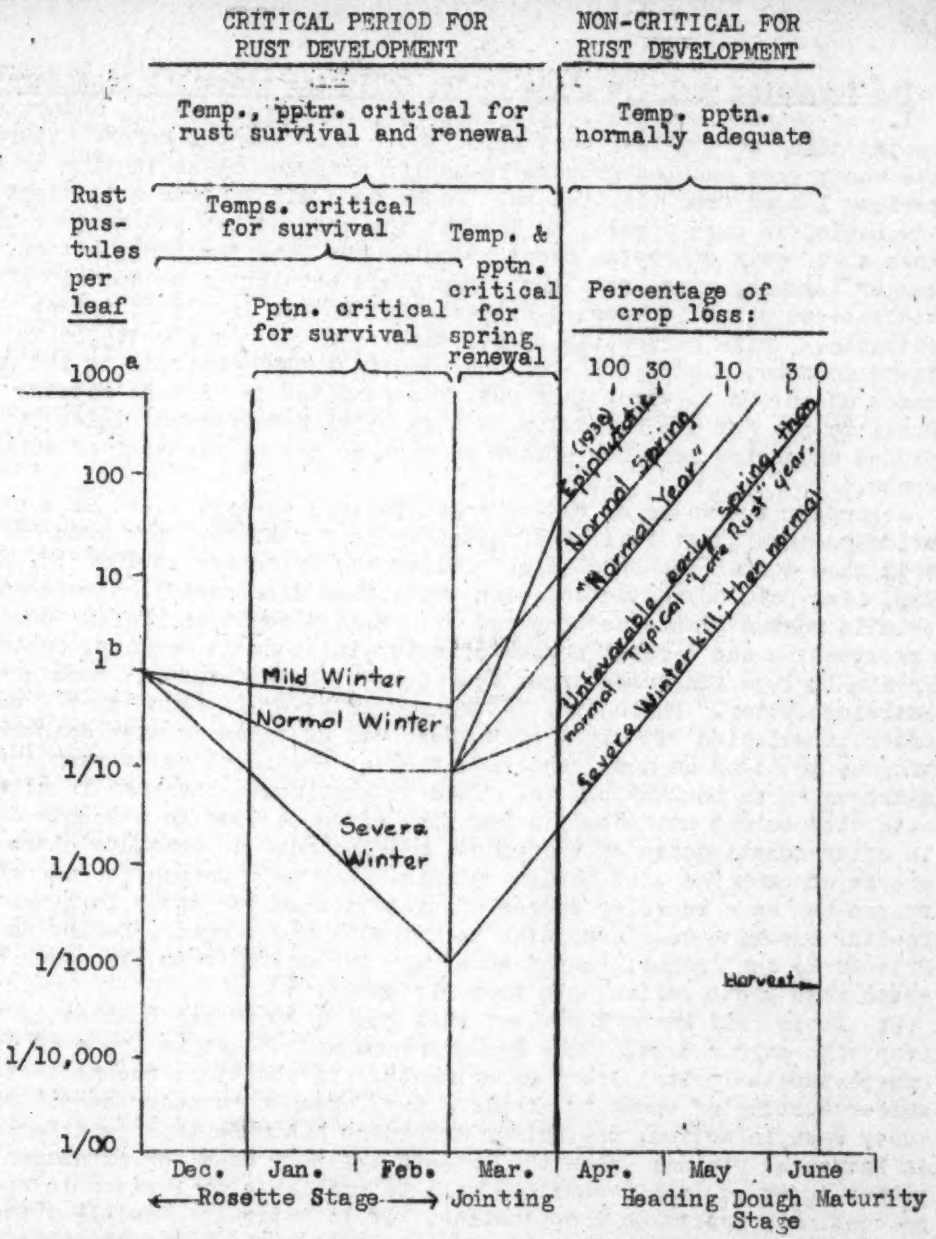

Figure 1. Diagrammatic representation of the effect of late winter weather in influencing the destructivensss of wheat leaf rust. Discussion in the text. Notes: a, 1000-pustule stage in which virtually all leaf tissue has been destroyed; in passing through fields one's clothes are reddened by the great quantities of uredospores; b, stage in which rust usually becomes noticeable to the casual observer.

The foregoing analysis leads to the following practical considerations:

1. As pointed out previously (Pl. Dis. Rep. 26:213-217), assurance of an impending severe leaf rust epiphytotic 2 1/2 months before maturity of the wheat crop enables growers to modify cropping plans in time to avert serious losses from the disease. Under some circumstances it might prove advisable, in such a case, to harvest the crop as hay and recover the loss that would otherwise occur by using the land for corn, cotton, or summer legumes, since some such crop could be planted seasonably after the date on which it becomes evident that severe leaf rust losses are inevitable. While harvesting rusted wheat for hay may seem to be an extreme measure, such salvage of the crop is amply justified by the many cases on record in which leaf rust has resulted in harvest returns too small to pay for the harvesting and in which unharvested fields have been plowed under too late for either salvage as hay or planting of substitute crops.

Regarding the value of rusted wheat foliage as hay, there is convincing evidence that wheat foliage affected by leaf rust contains much more protein than normal wheat foliage. Bolley and Pritchard in 1906 (N. D. Agr. Exp. Sta. Bul. 68) cited Canadian tests that disclosed 7.65 percent protein in rusted plants as compared with 2.44 percent in healthy ones. In an extensive and careful series of determinations in Germany, Gassner and Franke in 1930 (Untersuchungen über den Stickstoffhaushalt rostinfizierte Getreideblätter. Phytopath. Zeitschr. 11:517-570.) found that 3 weeks after inoculation with leaf rust there was 21 times as much soluble nitrogen, 10 times as much protein nitrogen, and 16 times as much total nitrogen as in healthy plants. This proportionate increase in nitrogen with disease was not merely a relative increase (due to absolute decrease in other constituents of the plant) but included an absolute nitrogen increase as compared with healthy plants. For this reason the use of leaf-rusted hay as a superior source of protein deserves study in livestock feeding experiments. According to Eriksson and Henning, Bolley and Pritchard, and Arthur, rusted wheat hay is non-toxic to livestock and is eaten with great relish when properly cured.

2. It is well known that leaf rust can be combatted by dusting the crop with sulfur dust. This has great value in certain types of agronomic and phytopathological field experiments. In addition, recent tests of sulfur dusting of wheat by airplane have shown that under conditions of heavy rust infection, the sulfur treatment has more than paid for itself in increased yields. When the present military need for airplanes and pilots is ended, their services will be available to farmers in such peace-time pursuits as crop dusting. It is entirely possible that in the course of time, in localities and seasons of ample rainfall, when potential yields are high and the cost of the dust treatment represents a proportionately small part of the potential harvest value, sulfur dusting of cereals will become adopted as a standard agricultural practice.

Workers who have experimented with sulfur dusting for rust control have frequently noted that rust control and yield increases from dusting are not appreciable if the dust is not applied well before the disease becomes abundant. The foregoing analysis of the relation of late winter weather to leaf rust indicates the reason for this. According to this analysis the dust applications in late winter, when the crop is in the

rosette stage and leaf rust is present only in very small amounts, may be expected to have greatest rust-preventive effect, and this should be considered in experimental or practical cereal dusting. Not only is this the most important period for checking rust development, but it is also a period at which the cost of the chemical is lowest, since there is less foliage to be protected than later in the season.

3. In tests to determine varietal or strain resistance of wheat genotypes, in connection with breeding for leaf rust resistance or attempts to include such resistance in developing improved wheat varieties, it becomes necessary in dry seasons to resort to artificial watering in order to induce sufficient rust so that rust observations in the nursery are significant. Since adequate moisture in late winter has been found indispensable to severe leaf rust development, while the rainfall of the spring months is normally adequate for such development, it follows that the greatest effect of artificial watering in experimentally increasing the rust will be obtained in correcting late-winter water deficits, e.g. in February and March in the latitude of Oklahoma, rather than in attempting to remedy such deficits by applying water as the crop approaches maturity.

Summary

That the subsequent intensity and destructiveness of wheat leaf rust (Puccinia triticina Eriks.) is determined almost entirely by the temperatures and precipitation of late winter (December through March in Oklahoma; December through April in Illinois and Iowa), and that the weather of the two following spring months, those in which rust becomes obvious, has very little decisive effect on leaf rust development, is shown to be the case in 16 principal leaf rust years and 17 principal years of relative freedom from leaf rust in Oklahoma, Illinois, and Iowa. This also explains the apparently inconsistent relationship of spring weather to rust in the Southwest in 1942 and 1943 and in Illinois in 1922-1926. This seemingly paradoxical weather-rust relationship is due to the fact that leaf rust must increase from its lowest winter prevalence by a logarithmic series of uredinial generations. The first of these generations occur in late winter at a time when the absolute amount of rust is so small that it is not apparent to the casual observer. In this period temperatures and precipitation are so near the lower threshold permitting rust multiplication that minor deviations of weather turn the balance in favor of or against rust multiplication. This determines the prevalence of rust at the opening of spring, after which time weather deviations have little effect in accelerating or retarding the logarithmic increase of rust, since the norms of precipitation and temperature in the spring are so far within the optimal range for leaf rust reproduction that seasonal variations are not great enough to markedly alter the course of rust multiplication.

Practical considerations resulting from the foregoing analysis include: (1) use of rusted wheat, which contains more protein than normal wheat, as hay, with utilization of wheat land for a summer crop during years in

which epiphytotic leaf rust is indicated by the end of the late winter period; (2) attention to the importance of the late winter period in schedules for applying sulphur dust for experimental or practical rust control; and (3) importance of the late winter period in artificial watering to induce local leaf rust epiphytotics in wheat variety testing nurseries.

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